

99 Pacific Street, Suite 155C  
Monterey, CA 93940 USA

+1.831.643.9266  
[OCEANA.ORG](http://OCEANA.ORG)

November 14, 2017

Mr. Lyle Enriquez  
National Marine Fisheries Service West Coast Region  
501 W. Ocean Blvd., Suite 4200  
Long Beach, CA 90802

**RE: Amendment 5 to the HMS FMP, Federal Drift Gillnet Permits (NOAA-NMFS-2017-0052)**

Dear Mr. Enriquez:

The National Marine Fisheries Service proposes amendment five to the Highly Migratory Species Fishery Management Plan (HMS FMP), which would “bring the State of California [limited entry drift gillnet] LE DGN permit program under Magnuson-Stevens Fishery Conservation and Management Act (MSA) authority.”<sup>1</sup> Oceana opposes the amendment because NMFS has not implemented hard caps on the serious injury or mortality of protected species in the fishery nor has the agency implemented 100 percent monitoring, as recommended by the Pacific Fishery Management Council (Council). What is more, we oppose the proposed federal permit program because it disregards key objectives outlined in the Council’s Swordfish Management and Monitoring Plan for achieving bycatch reduction goals and limiting drift gillnet fishing effort.<sup>2</sup>

Federal drift gillnet permits should only be issued upon implementation of the Council’s proposed management measures to establish protected species hard caps and 100 percent monitoring, as was the common understanding held by the Council and the public when the Council began discussing federalization of the permits and when it took final action. The agency’s withdrawal of the hard cap rule in June, and its failure to implement 100 percent monitoring, while at the same time moving ahead with the proposed federal permits, amounts to a ‘bait and switch’ by the agency, it undermines the State of California’s management of this fishery and it undermines the Council’s vision for a sustainable and clean West Coast swordfish fishery.

The need for federalizing the drift gillnet permits was defined by the Council’s Highly Migratory Species Management Team, as to avoid the phase out or prohibition of this gear type through “state bills” that “add[] a degree of uncertainty” and may “materially impair the Council’s ability to

---

<sup>1</sup> 82 Fed Reg. 43,323 (September 15, 2017).

<sup>2</sup> PFMC 2015. Pacific Coast Swordfish Management and Monitoring Plan. DRAFT. Agenda Item G.2. Attachment 1. September 2015.

manage the fishery.”<sup>3</sup> What has been made clear, however, is that the agency does not intend to follow through on the Council’s plans to manage the drift gillnet swordfish fishery. In fact, it is the agency’s actions that seem to impair the Council’s ability to manage the fishery.

We request the agency not proceed with the proposed amendment and instead return this action to the Council to:

1. **Amend the purpose and need** for this action to describe a larger vision for a sustainable West Coast swordfish fishery rather than the articulated purpose of expediency and avoiding state legislation.<sup>4</sup> The purpose and need should reflect Council goals to minimize bycatch of finfish and protected species (including sea turtles, marine mammals, and seabirds), limit drift gillnet fishing effort, and develop a deep-set buoy gear fishery as a clean alternative gear type.
2. **Reduce latency.** Federal drift gillnet permits should only be issued to active California drift gillnet permit holders. The Council’s Swordfish Monitoring and Management Plan discussed a federal DGN permit program in the context of “limiting fishing effort in the drift gillnet fishery.”<sup>5</sup> This included determining the “appropriate number of federal limited entry permits based on the bycatch reduction goal,” considering “how a federal limited entry permit could facilitate transitioning DGN fishery participants to other gear types” and investigating “mechanisms to compensate state permit holders that do not qualify for a federal permit.”<sup>6</sup> The proposed action, however, does none of this and instead would issue a federal DGN permit to all state DGN permit holders. The notice states that for the 2016-17 season, 70 California drift gillnet permits were issued and 67 have been issued for the 2017-18 fishing season.<sup>7</sup> However, there have been 20 or fewer active fishermen over the past five years.<sup>8</sup> Federalizing all latent drift gillnet permits risks increasing drift gillnet fishing effort with great increases in bycatch.
3. **Make clear that no additional federal drift gillnet permits shall be issued after the initial limited allocation.** The amendment language states that “If the permit expires, it will be

---

<sup>3</sup> PFMC September 2016. Agenda Item J.5.a HMSMT Report, at 1.

<sup>4</sup> Id. “The purpose of the proposed action is to rapidly and simply transition DGN permitting to MSA authority,” and the stated need is to circumvent “state bills” that “have been introduced which would materially impair the Council’s ability to manage the fishery.”

<sup>5</sup> PFMC 2015. Pacific Coast Swordfish Management and Monitoring Plan. DRAFT. Agenda Item G.2. Attachment 1. September 2015.

<sup>6</sup> Id.

<sup>7</sup> 82 Fed Reg. 43,323, 43,324 (September 15, 2017).

<sup>8</sup> PFMC September 2016. Agenda Item J.5.a HMSMT Report, at 3, showing 20 or fewer fishermen over the past 5 years. Figures 1 and 2a.

forfeited and NMFS will not reissue the permit to anyone.”<sup>9</sup> It should also be made clear that NMFS will not issue new permits to anyone now or in the future.

4. **Make federal drift gillnet permits non-transferable.** Under the proposed amendment, a permittee may transfer a federal drift gillnet permit after holding it for three or more years. To sunset swordfish drift gillnets and to promote other gear that minimizes bycatch, we request the agency make federal drift gillnet permits non-transferable.
5. **Connect the federal drift gillnet permit program with authorization of deep-set buoy gear.** When NMFS and the Council act to authorize deep-set buoy gear later in 2018, initial permitting should be exclusive to those individuals who have developed and pioneered deep-set buoy gear and to active swordfish drift gillnet permit holders that are willing to exchange their permit for deep-set buoy gear permits. It is critical that the agency establish a permitting system that enables this voluntary trade-in option as an incentive to fish with selective gear.
6. **Implement protected species hard caps and 100 percent monitoring.** In September 2015, the Council recommended adopting rolling two-year hard caps on the number of certain whale, dolphin and sea turtle species incidentally killed or injured by the California drift gillnet swordfish fishery. The Council also recommended that NMFS maintain a minimum 30 percent observer coverage level and/or require electronic monitoring, remove the unobservable vessel exemption, and establish 100 percent monitoring by 2018. These actions were taken to minimize bycatch, reduce impacts on non-target species, promote accountability and to set a clear standard for unacceptable bycatch amounts in the DGN swordfish fishery. While first supporting the proposed hard caps, NMFS withdrew the proposed rule in June 2017, contravening the will of the Council and the many members of the public who want to see an end to the killing of whales, dolphins and turtles.
7. **Discontinue efforts to allow drift gillnets into the Pacific Leatherback Conservation Area (PLCA).** Pacific leatherback sea turtles are at great risk of extinction and drift gillnets are a major threat to their continued survival and recovery. We urge the agency to discontinue consideration of any exempted fishing permits or boundary modifications that would allow this gear into the PLCA. A new scientific analysis found the temporal extent of the PLCA (August 15 to November 15) is the “shortest and most effective for protecting the turtles while allowing fishing during low bycatch risk periods.”<sup>10</sup> The authors concluded that a dynamic ocean management approach that would allow drift gillnets inside the PLCA while avoiding migrating and foraging leatherback sea turtles is not

---

<sup>9</sup> NMFS 2017. HMS FMP Amendment 5 language, section 6.2.5 and 82 Fed Reg. 43,323, 43,324 (September 15, 2017).

<sup>10</sup> Eguchi, T., S.R. Benson, D.G. Foley and K.A. Forney. 2016. Predicting overlap between drift gillnet fishing and leatherback turtle habitat in the California Current Ecosystem. *Fisheries Oceanography*. 26:1, 17-33.

presently possible based on currently available data. Such an endeavor is greatly complicated by the highly variable nature of the California Current Ecosystem. Instead, alternative gear types like deep-set buoy gear show promise for profitably catching swordfish while avoiding protected species interactions.

At the time the Council took final action on this proposed amendment, concerns were raised by the State of California representative on the Council and by the Lieutenant Governor.<sup>11</sup> It is disappointing to see the agency work swiftly to create a federal DGN permit program when California opposes it at this time.<sup>12</sup>

Thus, we oppose Amendment 5 to the HMS FMP without implementing the above recommendations to achieve a sustainable swordfish fishery. Halting approval of Amendment 5 would give NMFS, the State of California, NGOs and drift gillnet swordfish fishermen an opportunity to discuss the merits of a DGN permit buyback program and a transition to more selective fishing gear.

Sincerely,



Ben Enticknap  
Pacific Campaign Manager & Sr. Scientist



Geoff Shester, Ph.D.  
California Campaign Director & Sr. Scientist

cc. Barry Thom, West Coast Regional Administrator, NMFS  
Phil Anderson, Chair, Pacific Fishery Management Council

---

<sup>11</sup> PFMC Agenda Item J.6.a, Supplemental CA Lt. Governor Report: Letter to Chuck Bonham, CDFW, from California Lt. Governor Gavin Newsom re: PFMC vote to cede California's DGN fishery to Federal oversight. (March 11, 2017).

<sup>12</sup> Bonham, C. (California Department of Fish and Wildlife) letter to Mr. Lyle Enriquez, NMFS regarding Amendment 5 to the HMS FMP. (November 7, 2017).



# Predicting overlap between drift gillnet fishing and leatherback turtle habitat in the California Current Ecosystem

TOMO HARU EGUCHI,<sup>1\*</sup> SCOTT R. BENSON,<sup>2</sup>  
DAVID G. FOLEY<sup>1,3†</sup> AND KARIN A. FORNEY<sup>4</sup>

<sup>1</sup>Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 8901 La Jolla Shores Drive, La Jolla, CA 92037, U.S.A.

<sup>2</sup>Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 7544 Sandholdt Rd, Moss Landing, CA 95039, U.S.A.

<sup>3</sup>Institute of Marine Sciences, University of California at Santa Cruz, 100 Shaffer Rd, Santa Cruz, CA 95060, U.S.A.

<sup>4</sup>Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 110 Shaffer Rd, Santa Cruz, CA 95060, U.S.A.

## ABSTRACT

Concern over bycatch of protected species has become a key factor in shaping fisheries management decisions. In 2001, the National Marine Fisheries Service established an annual closure of a large mesh drift gillnet fishery targeting swordfish from central Oregon to central California between August 15 and November 15 because of concerns of bycatch of endangered leatherback turtles (the Pacific Leatherback Conservation Area, PLCA). The spatio-temporal constraints of the PLCA were developed to encompass nearly all previously observed leatherback turtle bycatch events in the fishery. The PLCA has been effective at reducing bycatch of leatherback turtles but has reduced fishing opportunities. In this study, we examined whether the timing of the current PLCA closure is optimal for leatherback turtle conservation, by developing statistical models of leatherback turtle presence inside the PLCA based on environmental variables. We also examined finer-scale spatiotemporal patterns of potential overlap between the fishery and leatherback turtle foraging habitat using Maxent and Random Forests applied to logbook data and leatherback turtle telemetry data. Our results suggest that the temporal extent of the current static closure period is the shortest and most effective for protecting the turtles while allowing

fishing during low bycatch-risk periods. We also found that it is possible to predict foraging habitat of leatherback turtles and fishing effort using environmental variables. Identification of spatial and temporal hot-spots of potential overlap between fishing effort and leatherback turtle distribution can form a basis for dynamic management approaches.

**Key words:** bycatch, endangered species, fishery closure, fishery interactions, habitat modeling, swordfish, thresher sharks, U.S. west coast

## INTRODUCTION

Interactions between fishing operations and protected species have been considered a challenging issue throughout the world's oceans (Read *et al.*, 2006; Read, 2008; Wallace *et al.*, 2010). Many international forums and conferences have been convened to discuss bycatch reduction while maintaining fishing operations by organizations such as International Fishers Forum (<http://www.fishersforum.net/>), American Fisheries Society (<http://www.fisheries.org>), and National Marine Fisheries Service (<http://www.nmfs.noaa.gov>). Although gear modifications, time-area closures, and acoustic deterrents have reduced bycatch of some species in particular fisheries (e.g., Gilman *et al.*, 2005, 2006, 2008; Cox *et al.*, 2007; Larsen *et al.*, 2007; Carretta *et al.*, 2008), bycatch reduction remains a global management challenge (e.g., Alverson *et al.*, 1994; Rivera and Wohl, 1999; Eayrs, 2007) that is complicated by the lack of a unified international management framework for many fisheries and transboundary species, such as the leatherback turtle (*Dermodochelys coriacea*; e.g., Dutton and Squires, 2011; Curtis *et al.*, 2015; Komoroske and Lewison, 2015).

In the U.S., the National Marine Fisheries Service (NMFS) is responsible for sustainably managing diverse marine species, including invertebrates, fishes, marine mammals and turtles, under the Magnuson-Stevens Act (MSA), Marine Mammal Protection Act (MMPA), and Endangered Species Act (ESA). Bycatch is traditionally monitored via observer programs and/or logbooks, and such efforts have been helpful in characterizing fisheries-specific threats and

\*Correspondence. e-mail: tomo.eguchi@noaa.gov

†Deceased.

Received 2 May 2016

Revised version accepted 22 July 2016

management needs. However, logistical and economic constraints limit observer coverage to a fraction of the total fishing effort, and logbook records are known to be unreliable (e.g., Baker *et al.*, 2006; Read *et al.*, 2006; Sampson, 2011). Both of these factors contribute to uncertainty in bycatch estimates. Furthermore, for rare species with a low absolute bycatch rate, statistical estimates can be imprecise (Carretta and Moore, 2014). To reduce uncertainty in bycatch estimates, a variety of statistical techniques have been used to correct biases, control for confounding factors, and better understand the temporal and spatial distributions of observed bycatch (Gardner *et al.*, 2008; Sims *et al.*, 2008; Murray, 2009; Murray and Orphanides, 2013; Martin *et al.*, 2015).

While the above tools can help explain observed patterns and reduce uncertainty, different approaches are required to predict bycatch risk to unobserved times or places. Models that consider spatio-temporal variation in fishing behavior as well as the distribution of by-caught species provide a complete assessment of overlap and potential bycatch risk, because both can be dynamic as ocean conditions change (e.g., Forney, 2000; Ferguson *et al.*, 2005; Hobday and Hartmann, 2006; Block *et al.*, 2011; Forney *et al.*, 2011). For example, the distribution of marine predators is affected by the distribution of their prey species, which may, in turn, be affected by time, static physical features, and dynamic ocean features such as ocean currents, productivity, or water temperature. The distribution of fishing effort may also relate to such environmental cues, as fishermen seek to maximize catch per unit effort based on their knowledge, but other factors such as regulations, fuel and labor costs, the distributions of target species, and the size of fishing vessels also play a role (Soykan *et al.*, 2014).

Telemetry data, when available, can be useful for inferring relationships between species distributions or behavior and environmental conditions or bycatch risk (Jonsen *et al.*, 2003; Morales *et al.*, 2004; Hobday and Hartmann, 2006; Johnson *et al.*, 2008; Seminoff *et al.*, 2008; Benson *et al.*, 2011; Dewar *et al.*, 2011; Shillinger *et al.*, 2011; Zydalis *et al.*, 2011; Roe *et al.*, 2014). Telemetry and fishery data can also provide a basis for developing near real-time management tools to reduce bycatch, e.g., the TurtleWatch products for the Pacific loggerhead (*Caretta caretta*) and leatherback turtles (Howell *et al.*, 2008, 2015). Such dynamic ocean management approaches are increasingly recognized as valuable tools to achieve sustainable fisheries that balance marine resource use and conservation concerns (Lewison *et al.*, 2015; Maxwell *et al.*, 2015). For example, dynamic management might reduce

fishing effort or restrict gear types only when species of concern are expected to be present in a specific area of interest. If these species are rare, the ability to predict their overlap with fishing activity can be difficult.

In this study, we develop predictive models of fishing effort for the US west coast drift gillnet fishery (the DGN fishery hereafter) and the distribution of endangered leatherback turtles off the U.S. west coast to evaluate the current regulatory measures and evaluate the potential for dynamic management of this fishery in the future. Leatherback turtles are found along the US west coast during summer and autumn, when dense aggregations of jellyfish, especially the brown sea nettle (*Chrysaora fuscescens*), are common (Graham *et al.*, 2001, 2010; Benson *et al.*, 2007, 2011). Telemetry studies have revealed that these leatherback turtles are part of the Western Pacific nesting population, which has experienced a dramatic (~80%) decline in abundance during the past three decades (Tapilatu *et al.*, 2013).

The DGN fishery targets swordfish (*Xiphias gladius*) and common thresher sharks (*Alopias vulpinus*). The fishery uses a panel of netting suspended vertically in the water, while the net is attached to a vessel at one end and drifts along with the current. Nets are typically set in the evening, allowed to soak overnight, and retrieved in the morning, where the average soak time is approximately 10 h. Although the DGN fishing season is from August 15 to August 14 of the following year, nearly all of the fishing effort occurs from August 15 to January 31 of the following year (National Marine Fisheries Service, 2013). The DGN fishery is managed federally and requires a permit, which is linked to an individual fisherman. The number of permits has declined from 251 in 1986 to 78 in 2000, and by 2012, only 16 vessels actively participating in the DGN fishery. Fishing effort has declined from approximately 10 000 annual sets in the mid-1980s to fewer than 500 in recent years, whereas approximately 15% of all sets have been observed since 1990 (Carretta and Barlow, 2011; NMFS unpublished data). There were 25 observed incidental captures of leatherback turtles in the DGN fishery between 1990 and 2014.

To reduce bycatch of leatherback turtles in the DGN fishery (Julian and Beeson, 1998; Carretta *et al.*, 2004), NMFS established the Pacific Leatherback Conservation Area (PLCA, Fig. 1) in 2001. The PLCA extends from central Oregon to central California and is closed to DGN fishing annually from August 15 to November 15 (50 CFR Part 660). There have been two entanglements of leatherback turtles, both of which were released alive, in the DGN fishery since

the PLCA was established (Carretta *et al.*, 2014). While this closure has been very effective for reducing leatherback turtle bycatch, it is also restrictive to the fishery, and there may be opportunities for the fishery via dynamic ocean management (Maxwell *et al.*, 2015) given the variable nature of the California Current Ecosystem (Chelton *et al.*, 1982) and variability in leatherback turtle movements and habitat use in this area (Benson *et al.*, 2011).

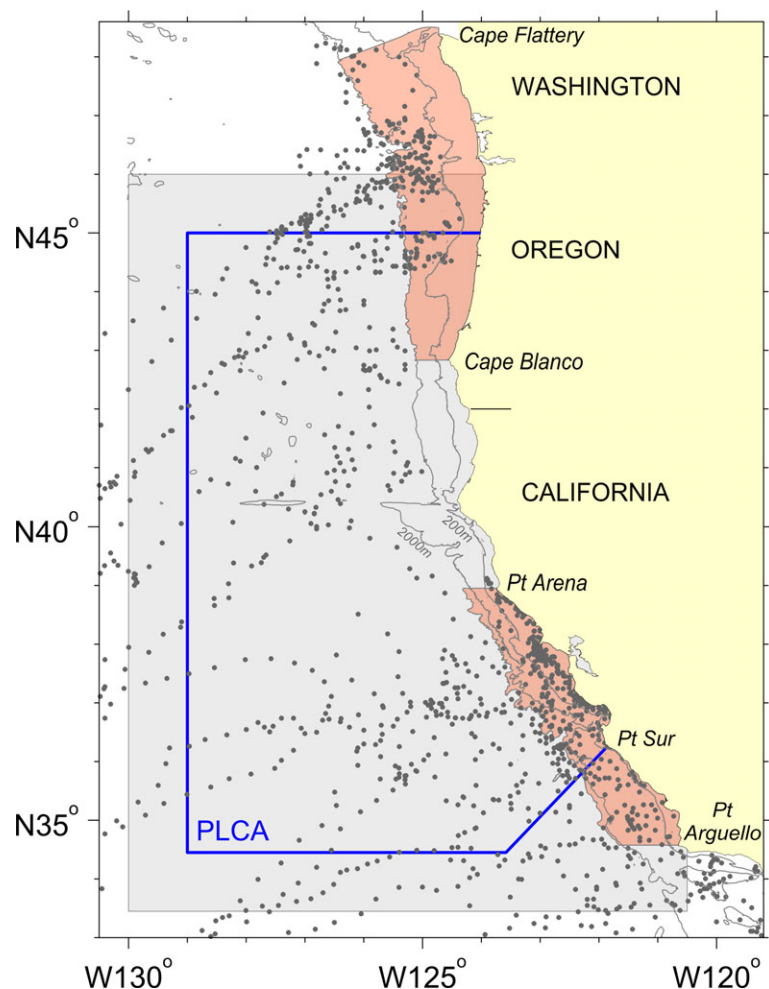
To examine the feasibility of dynamic management of leatherback turtle bycatch in this fishery, we had two primary objectives. First, we used telemetry data to develop habitat-based predictive models of leatherback turtle presence in the PLCA, which were used to evaluate whether the same level of leatherback turtle protection as the current static closure might be achieved with a closure period based on statistical predictions. Second, we developed spatio-temporal models of inferred leatherback turtle foraging habitat, DGN fishing effort, and their respective overlap at

0.5 degree spatial and 14-day temporal resolutions. This second objective was intended as a feasibility study to examine whether finer-scale dynamic management of the DGN fishery may be possible. We show that the current PLCA closure timing is appropriate and that co-occurrence of foraging habitat and DGN effort can be predicted at the examined spatio-temporal scale. These results provide a foundation for future research, such as model-based bycatch simulations, to evaluate potential dynamic management strategies that would increase fishing opportunities while maintaining protection of leatherback turtles and other species.

## METHODS

### Study area

To investigate the potential overlap between the DGN fishery and leatherback turtles, we defined our study area to be a polygon bounded by 33.45°N,



**Figure 1.** Telemetry data points (dark gray filled circles), depth contours, assumed foraging areas (light red), study area boundaries (light gray), and the Pacific leatherback conservation area (PLCA).

46.00°N, 130.00°W and the west coast of the US (Fig. 1). This area is part of the California Current Ecosystem (CCE; Mann and Lazier, 2006), which is one of the most productive marine ecosystems in the world. The California Current is a southward-flowing eastern boundary current that originates in the Gulf of Alaska and flows to the eastern equatorial Pacific. Primary productivity in the ecosystem is largely driven by wind-driven coastal upwelling in spring and summer, which brings nutrient-rich water to the surface followed by periods of relaxation of upwelling and resulting in phytoplankton blooms (Bakun *et al.*, 1974; Lynn and Simpson, 1987). CCE productivity is affected by seasonal, inter-annual, and decadal scale variability. Leatherback turtles are found most often during summer/autumn (July–October) in neritic waters corresponding to the period when upwelling relaxes, and sea surface temperature (SST) increases, but their abundance and distribution varies interannually (Starbird *et al.*, 1993; Benson *et al.*, 2007, 2011).

#### Data

*Leatherback turtle telemetry data.* The satellite-linked telemetry data in this study were a subset of those used in Benson *et al.* (2011). These tracks had been filtered using the switching state-space model developed by Jonsen *et al.* (2005). We selected those tracks that had positions in our study area but excluded departure tracks for leatherback turtles that exhibited a flight response immediately after being tagged in nearshore waters off California (Benson *et al.*, 2011). A total of 15 individual tracks with 973 location points from 2001 to 2008 were included in this study (Figure 1).

Two datasets were created from the telemetry location data for the two separate objectives of this study. The first dataset was used to predict the timing of leatherback turtle presence in the PLCA. Telemetry locations were categorized as inside or outside the PLCA (presence and absence, respectively). To consider the possibility that different environmental variables affected entry to and departure from the PLCA, we further separated this dataset into ‘entry’ and ‘departure’ data subsets. Telemetry data indicated that leatherback turtles would enter in the area by August, whereas they would leave the area in late autumn, responding to local oceanographic conditions (Benson *et al.*, 2011). Consequently, the ‘entry’ data subset spanned from the July 1 to the September 30 and the departure subset spanned from the October 1 to the December 31. For all available entrances and departures in the telemetry data, the 30 days before and after were considered as ‘absences’ (Fig. 2). Statistical

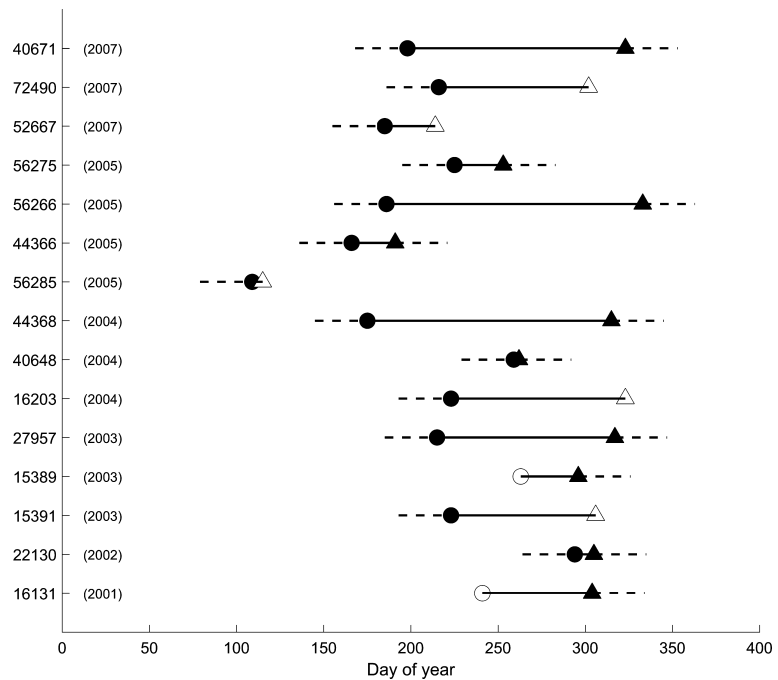
models were fitted separately to the entry and departure data subsets.

The second dataset was used to develop a predictive spatial model of inferred leatherback turtle foraging habitat in the PLCA. The PLCA includes portions of two foraging areas that have been designated as a critical habitat for leatherback turtles under the ESA (2012; 77 Federal Register 4170; January 26, 2014): (1) neritic waters off central California between Point Arena (38.909°N 123.693°W) and Point Arguello (34.577°N 120.647°W) extending offshore to the 3000-m isobath, (2) nearshore waters between Cape Flattery (48.383°N 124.714°W), Washington, and Cape Blanco (42.836°N 124.564°W), Oregon, extending offshore to the 2000-m isobath. Benson *et al.* (2011) determined a greater probability of foraging in these areas. For our feasibility study, we assumed that telemetry positions within either of these critical habitat areas were associated with foraging behavior, whereas those outside of these areas were associated with non-foraging behavior. These data were used to develop models to predict foraging habitat of leatherback turtles using associated environmental variables. We note that leatherback turtles may also be at risk of bycatch when they are not foraging, but habitat associations differ for foraging and non-foraging behavior (Benson *et al.*, 2011). We chose to model foraging habitat as a simple case study to evaluate the potential for spatio-temporal predictions of overlap between leatherback turtles and the DGN fishery. If successful, this would provide a foundation for a more comprehensive bycatch risk analysis that takes into account non-foraging behavior as well.

*The DGN fishery.* The DGN fishery dataset used to model fishing effort consisted of the number of sets in 10' × 10' blocks within our study area from 1990 to 2000 (before implementation of the PLCA), extracted from logbook records managed by NMFS. Although logbook records are available as far back as 1981, these earlier data could not be included in our model because the availability of environmental variables was limited before 1990. The pooled 1990–2000 DGN fishery data form the basis for a predictive model of fishing effort distribution, with the assumption that these data are representative of the underlying mechanisms affecting fishing locations during other years. The model was then used to predict what the distribution of fishing effort might have been during 2001–2010 if the PLCA were not in place, and to examine potential overlap with the 2001–2010 leatherback turtle foraging habitat model.



**Figure 2.** Data for the presence of leatherback turtles in the PLCA determined by the telemetry data (n = 15). Solid lines indicate presence and dashed lines indicate absence. Filled circles indicate entry dates, open circles indicate tagged dates, open triangles indicate dates when transmission ceased within the PLCA, and filled triangles indicate departure dates. Animal identification numbers on the vertical axis and years are in parentheses.



*Environment.* Different environmental variables were used for the two objectives of the study, because the first objective addressed a temporal question (timing of leatherback turtle presence in the PLCA), whereas the second set of models required spatio-temporal habitat information. Temporal variables for the first objective included the upwelling index (UW) at latitudes 36°N, 39°N, 45°N and 48°N (Bakun, 1973; Schwing and Mendelsohn, 1997; Bograd *et al.*, 2009), the Northern Oscillation Index (NOI; Schwing *et al.*, 2002), the Pacific Decadal Oscillation Index (PDO; Mantua *et al.*, 1997) and the day of the year (DOY). UW and NOI were obtained from the NOAA Fisheries, Environmental Research Division<sup>1</sup>, whereas PDO was obtained from the Joint Institute for the Study of Atmosphere and Ocean<sup>2</sup>. Possible cumulative effects or time lags over time were considered by extracting the indices over 30, 60, and 90 days before each telemetry data point and computing the mean, standard deviation (s), and cumulative (cumu) values. Variables were defined as follows: abbreviated variable name, latitude, statistic, and lag period. For example, UW36s\_60d indicates the standard deviation of UW index at 36N over 60 days.

For the second objective, i.e., to predict the distributions of leatherback turtle foraging habitat and the DGN fishery, nine spatio-temporal environmental

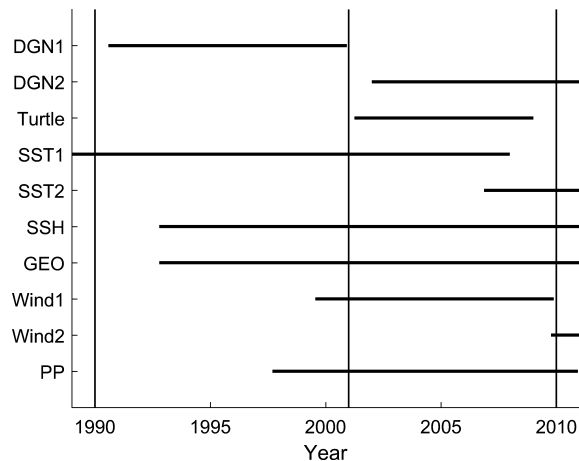
variables were selected based on the results of Benson *et al.* (2011): primary productivity (PP), SST, total kinetic energy (TKE), wind-driven upwelling (WEKM), sea surface height (SSH), sea surface height variability (SSHV), sea surface height anomaly (SSHA), and meridional and zonal geostrophic current speed (UGEO and VGEO, respectively). These data were acquired from the data access website of NOAA Fisheries, Environmental Research Division<sup>3</sup> using Matlab (MathWorks Inc., Natick, MA, USA) routines available from the same website. All variables were acquired at their native resolutions but aggregated to match our prediction resolution of 0.5 × 0.5-degree polygons. Primary productivity data (mg C m<sup>-2</sup> day<sup>-1</sup>) were 8-day composites (MODIS; Fig. 3). SST data (°C) were 8-day composites from two different sources [Advanced Very High Resolution Radiometer (AVHRR) and MODIS/GOES/AVHRR] available for two different periods (Fig. 3). Geostrophic current data (m s<sup>-1</sup>) in meridional (U) and zonal (V) directions were obtained from altimetry sensors on various satellites. TKE was computed as ½(U<sup>2</sup> + V<sup>2</sup>) (Ducet *et al.*, 2000). WEKM is a measure of wind-driven upwelling from wind stress (Xie and Hsieh, 1995). SSH (m) were obtained from altimetry sensors aboard multiple satellites (Table 1). SSHV is the root mean square in SSH within each cell (0.5 × 0.5 degrees) and SSHA is

<sup>1</sup><http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/>

<sup>2</sup><http://research.jisao.washington.edu/pdo/PDO.latest>

<sup>3</sup><http://coastwatch.pfeg.noaa.gov/erddap/index.html>

**Figure 3.** Temporal availability of various environmental data that were used in predicting leatherback foraging habitat and DGN locations. Vertical lines indicate the beginning of observer coverage (1990), establishment of time-area closure (2001), and end of predictions (2010). See Table 1 for abbreviations and data sources.



the difference between the observed SSH and the long-term average. For the 1990–2000 DGN fishery, we used static variables (latitude, longitude, depth, and day of the year) combined with SST as the only dynamic variable because fewer dynamic variables were available (Fig. 3). Depths (m) were obtained from the NOAA National Geophysical Data Center website. We also considered possible effects of time lag (8, 14 or 30 days) between oceanographic variables and turtle/fishery habitat; for example, the 8-day lagged data for the second half of August 1995

(August 15–31) would consist of environmental data from August 7–23, 1995.

Throughout this manuscript, spatial environmental variables are abbreviated in the following manner: abbreviated variable name (e.g., SSH) followed by statistic, then time lag. For example, SSHs\_30d would indicate the standard deviation of SSH over 30 days.

#### Predictive models

Different analytical tools were used for the three different predictive models (presence of leatherback turtles in the PLCA, foraging habitat of leatherback turtles, and DGN fishing locations), because of differences in the available data and their statistical properties. Each will be described separately below.

*Presence of leatherback turtles in the PLCA.* The temporal presence and absence of leatherback turtles in the PLCA was modeled using a mixed effects logistic regression framework. First, however, we determined the variables that were useful in modeling the presence/absence of leatherback turtles in the PLCA for entry and departure separately using a conditional Random Forests (RF) classification approach (*cforest* in R package *party*; Hothorn *et al.*, 2006; Strobl *et al.*, 2007, 2008) in the R statistical environment (R Core Team 2014). Because specific locations were not used in this analysis (i.e., we examined only whether or not a particular telemetered location was inside of the PLCA), data were treated as a binary response. The performance of the RF model was evaluated using the confusion matrix (R package *caret*; Kuhn 2013) on

**Table 1.** Environmental variables used for modeling leatherback turtle foraging habitat, their abbreviations, source satellite, and sensor names in parentheses.

Variable name (abbreviation)	Satellite (sensors)
Sea Surface Temperature (SST)	
SST1	NOAA-17 and NOAA-18 polar orbiting spacecraft (AVHRR)
SST2	Aqua (MODIS, Aqua), NOAA GOES-10, GOES-12 (GOES), NOAA POES-17, and POES-18 (AVHRR)
Geostrophic current (UGEO and VGEO)	TOPEX/Poseidon, ERS-1, ERS-2, Geosat Follow-On, Envisat, Jason-1 (Altimeter)
Wind (wekm)	
Wind1	QuikSCAT (SeaWinds)
Wind2	METOP (ASCAT)
Primary Productivity (PP)	GeoEye Orbview-2 (SeaWiFS), NOAA-POES (AVHRR) NASA Aqua (MODIS)
Sea Surface Height (SSH)	JASON-1, TOPEX/POSEIDON, ENVISAT, GFO, ERS ½, GEOSAT (Altimetry sensors on multiple spacecraft)

AVHRR, Advanced Very High Resolution Radiometer; MODIS, Moderate Resolution Imaging Spectroradiometer; AMSR-E, Advanced Microwave Scanning Radiometer; SeaWiFS, Sea-viewing Wide Field-of-view Sensor; ASCAT, Advanced Scatterometer; POES, Polar-orbiting Operational Environmental Spacecraft; QuikSCAT, Quick Scatterometer; METOP, Meteorological operational satellite.

out-of-bag predictions, which were the predictions for data points that were not used to build models. To evaluate the prediction accuracy, we used the kappa statistic ( $\kappa$ ; Cohen, 1960), which measured the proportional increase in predicted accuracy relative to an expected accuracy. Higher values indicated a better predictive performance.

In the RF approach, variable importance can be determined using two measures: (1) how prediction error changes when a variable is randomly permuted (Breiman, 2001) and (2) how area under the receiver operator characteristics (AUC curve) changes when a variable is randomly permuted (Janitza *et al.*, 2013). In addition to these variable importance measures, we added a random number variable, which consisted of random numbers from a uniform distribution between 0 and 100. Variables that were less useful in predicting the presence/absence of leatherback turtles in the PLCA than random numbers were discarded.

Using the variables identified as important by the RF analysis, we developed mixed-effects linear logistic regression models on presence/absence data, where individuals were treated as the random effect variable. The RF approach was not affected by correlations among predictor variables (Breiman, 2001), but the regression approach would have been affected. Consequently, pair-wise correlations were computed among the predictor variables and candidate logistic regression models were only allowed to include uncorrelated variables. Models were fitted to the data using a Bayesian approach (Bayesian linear mixed effects models, BLMM) using the *rjags* package (Plummer, 2015). Convergence was determined using the Gelman–Rubin statistic (Gelman *et al.*, 2014). The models were compared using approximate Deviance Information Criteria (DIC; Gelman *et al.*, 2014).

The selected models for entry and departure then were used to predict the median daily probability of the presence of leatherback turtles in the PLCA when the DGN fishery was operating in the area; 1990–1999. For each of these years, probabilities of turtle presence in the PLCA were computed for July 1 (DOY = 182) to September 30 (DOY = 273) using the entry dataset, for October 1 (DOY = 274) to December 31st (DOY = 365) using the departure dataset, and the medians of the posterior distributions.

*Foraging habitat of leatherback turtles.* To predict foraging habitat of leatherback turtles in the study area, we used an RF approach because it allowed us to mine our data without the need to eliminate correlated predictor variables (Breiman, 2001). Telemetry locations within the critical habitat areas (Fig. 1) were

considered to be ‘foraging’ and locations outside these areas were considered non-foraging. Analyses were performed using the *cforest* function in the *party* package (Hothorn *et al.*, 2006; Strobl *et al.*, 2007, 2008) in the R statistical environment. Although RF are not prone to overfitting and predictive power is increased by including as many variables as possible (Breiman, 2001; Hothorn *et al.*, 2006; Strobl *et al.*, 2007, 2008), we strived to build parsimonious models. Therefore, useful variables for predicting foraging habitat were selected using the same variable selection process described above. Model predictions of leatherback turtle habitat were then made for the years 2001–2010 at a  $0.5 \times 0.5$ -degree spatial resolution and 14-day temporal resolution.

*DGN fishing locations.* The DGN fishery prediction required a different approach (Maxent; Phillips *et al.*, 2006; Phillips and Dudik, 2008) because logbook data only provided presence locations. Ideally, Maxent analyses should encompass the full range of environmental conditions (background) available to the fishery and sample the background with a similar bias as the presence points (Phillips *et al.*, 2009; Elith *et al.*, 2011). Because we did not have a means to sample background data as fishers selected their set locations, we selected the background environmental data systematically from a grid. The spatial distribution of DGN fishing was modeled as a function of latitude, longitude, day of the year (DOY), depth, and SST with possible effects of time lag (8, 14, and 30 days). As for the leatherback turtle data, we used random numbers to evaluate the usefulness of environmental variables for predictions. After determining variables that were more useful than random numbers, models were rebuilt using only those variables.

Maxent modeling requires a few parameters to be set, including prevalence, regularization parameter, and features. The prevalence parameter ranges from 0 to 1 and represents the probability of presence given the environment (Elith *et al.*, 2011). Therefore, in general, the parameter should be set according to the abundance of the species; larger values for abundant species and vice versa. The particular value of prevalence becomes important when multiple species of various abundances are compared in predicted probabilities of occurrence using the Maxent approach (Elith *et al.*, 2011). The default value of 0.5, however, is often used when abundance information is lacking. Because we pooled data for all years and we were not comparing among multiple species, we used the default value of 0.5. The regularization parameter in Maxent penalizes complex models, but there is no particular

value that can be used for all analyses. It has been recommended that a user needs to explore different values of the regularization parameter. Smaller values fit the data well but may have less applicability to new data. Following the advice in Phillips and Dudik (2008), we tested various values of the regularization parameter (0.05, 0.1, 0.22, 0.46, and automatic selection). Only two of the available features in the Maxent package (linear, quadratic, polynomial, hinge, and threshold), were allowed in each model for simplicity and interpretability. Among all possible combinations, we considered the following six: linear + quadratic (LQ), linear + polynomial (LP), linear + threshold (LT), hinge + quadratic (HQ), quadratic + threshold (QT), and hinge + threshold (HT).

To compare the performance of models, four-fold cross-validations were used to develop models on  $\frac{3}{4}$  of the total dataset (training data) and to test the fit on the remainder (test data). All combinations (30) of five regularization parameters and six features were compared using three statistics on test data; gain, AUC, and prediction power. The gain in Maxent is the average log probability of the presence samples. Therefore, gain, or  $\exp(\text{gain})$  to be exact, provides a metric of how much greater the average likelihood was at the presence datum compared with a random background point (Phillips *et al.*, 2006). The AUC in the Maxent modeling approach is interpreted as the probability that a randomly selected presence data point is ranked above a random background site (Phillips *et al.*, 2006). Finally, we used a confusion matrix, especially the probability of correctly predicting the presence of DGN fishing in the test data (sensitivity), as the third measure of model performance.

In addition to these statistics, we used response curves of explanatory variables to select feature combinations that were not overly complicated. In other words, feature combinations with response curves with many ‘wiggles’ were avoided even if the model selection statistics (gain, sensitivity, and AUC) indicated good fits. The best combination of a model and a set of variables through this process was used for predictions of the relative DGN fishing likelihood of the  $0.5 \times 0.5$ -degree polygons over 14-day periods in the years without fishing data, i.e., after 2000. All Maxent analyses were conducted using Maxent software (v. 3.3.3k; Phillips *et al.*, 2006) through the *dismo* package (v. 1.0.5; Hijmans *et al.*, 2014) in the R statistical environment.

*Co-occurrence of leatherback turtles and DGN fishing.* To predict the co-occurrence of leatherback turtle habitat and the DGN fishery, we predicted turtle

habitat and fishing effort distribution on the same temporal (14-day periods between August 15 and November 15 from 2001 to 2010) and spatial scales ( $0.5 \times 0.5$  degree polygon). We then averaged over the 10-yr period to create average co-occurrence likelihoods for each 14-day period. It is important to note that a high likelihood of leatherback turtle habitat (or DGN fishing location) does not equate to a high density of turtles (or DGN presence) because it is affected by the abundance of turtles (or DGN fishing vessels) in the area. As an extreme example, if there were one leatherback turtle (or DGN fishing vessel) in the area, even if there were many areas of predicted foraging (or fishing) habitat, no more than one can be occupied by the turtle (or the fisher) at any given time. Nonetheless, the product of the likelihoods of leatherback habitat and fishing activity within each  $0.5 \times 0.5$ -degree polygon provides a relative measure of bycatch risk, because the two processes are independent of one another.

## RESULTS

### *Presence of leatherback turtles in the PLCA (logistic regression)*

*Entry to the PLCA.* According to the RF variable importance measures, the most influential variables for the prediction of entry to the PLCA by leatherback turtles were standard deviation (s) and cumulative sum (cumu) of upwelling indices (UW) at 36 and 39°N (UW36s\_90d, UW36s\_60d, UW36cumu, and UW39cumu, where 60d and 90d refer to time lags of 60 and 90 days, respectively). The RF model accurately predicted the presence/absence of leatherback turtles in the PLCA, yielding 87% of correct assignments and a  $\kappa$  statistic of 0.71. High pair-wise

**Table 2.** Model definitions and  $\Delta\text{DIC}$  values for modeling the entry of leatherback turtles into the PLCA using the BLMM approaches.

Model	Definition	BLMM $\Delta\text{DIC}$
4	UW36s_60d + UW39cumu	0.00
3	UW39cumu	204.24
1	UW36s_90d	298.41
2	UW36s_60d	324.85

BLMM = Bayesian linear mixed-effects model.  
UW36s\_60d and UW36s\_90d = standard deviation of upwelling at 36°N over 60 and 90 days, respectively;  
UW39cumu = cumulative upwelling at 39°N.

correlations were found between UW36cumu and UW39cumu (Pearson’s correlation = 0.96) and between UW36s\_60d and UW36s\_90d (Pearson’s correlation = 0.85). Therefore, using the only uncorrelated variables, four candidate models were developed, where Model 4 (UW36s\_60d + UW39cumu) was identified as the best based on DIC values (Table 2). Convergence of Markov chains for all models was confirmed via the Gelman–Rubin statistic (<1.01). The estimated coefficients indicated that the likelihood of leatherback turtles entering the PLCA was high when the standard deviation of the UW index over 60 days at 36N (UW36s\_60d) is small (negative coefficient) and the cumulative UW index at 39N (UW39cumu) is high (positive coefficient; Table 3). The estimated standard deviation for the random effects, i.e., individual-level variability, was 31.2 (95%PI = 19.2–53.9; Table 3).

*Departure from the PLCA.* The order of important variables for the departure dataset was different from that for the entry dataset. Various statistics for the upwelling index at 48°N were determined to be important. The prediction of departure from the PLCA using RF was accurate, yielding 96% of correct assignments and a  $\kappa$  statistic of 0.92. Pair-wise correlations of the six most important variables indicated that the top five variables were strongly correlated with each other. Consequently, we used the mean upwelling index at 48N over 60 days (UW48mean\_60d) and PDO to develop four candidate logistic regression models including an interaction between the two (Table 4). The DIC values indicated that Model 3, with both variables, was better than Model 4, which included an interaction between the two variables. PDO had a negative effect whereas UW48mean\_60d had a positive effect on the probability of leatherback turtles’ presence in the PLCA (Table 5). In other words, leatherback turtles departed the PLCA when the mean UW index over 60 days at 48°N (UW48mean\_60d) was low, and the PDO was high. The estimated standard deviation for the random effects, i.e., individual-level variability, was 9.12 (95%PI = 5.22–18.11), which was smaller than the same parameter for the entry dataset (31.2, 95%PI = 19.2–53.9; Tables 3 and 5).

Based on the combined entry and departure models, the median probability of leatherback turtle presence in the PLCA increased rapidly during mid-July, which was earlier than the beginning of the existing fishery closure (August 15; Fig. 4). The probability decreased in November and December in the 10-yr period from 1990 to 1999.

**Table 3.** Estimated coefficients and approximate 95% posterior intervals for the best logistic regression model (Model 4) for the analysis of predicting the entry of leatherback turtles to the PLCA.

Model 4	Median	2.5%	97.5%
Intercept	6.68	-7.39	19.72
UW36s_60d	-6.06	-11.02	-2.00
UW39cumu	30.50	22.02	40.55
s	31.16	19.17	53.85

UW36s\_60d = standard deviation of upwelling at 36°N over 60 days, UW39cumu = cumulative upwelling at 39°N, s = the standard deviation of the individual random effects.

**Table 4.** Model definitions and  $\Delta$ DIC values for modeling the departure of leatherback turtles from the PLCA using the BLMM approach.

Model	Definition	$\Delta$ DIC
3	UW48mean_60d + PDO	0.00
4	UW48mean_60d*PDO	34.12
1	UW48mean_60d	131.56
2	PDO	518.86

PDO = Pacific Decadal Oscillation Index. UW48mean\_60d = mean upwelling at 48°N over 60 days, The product model (Model 4) includes linear terms also, i.e., UW48mean\_60d + PDO + UW48mean\_60d:PDO.

*Foraging habitat of leatherback turtles (Random Forest)*

Among the environmental variables used in the analysis (i.e., SST, UGEO, VGEO, WEKM, PP, SSH, SSHV, SSHA, TKE, and DOY), all variables with various time lags were more important than random numbers. Although primary productivity (PP) appeared to be an influential variable, PP was not available at many times and locations because of cloud cover. Therefore, we selected an alternate model that included SST, SSH, and SSHV at various time lags and had the same predictive accuracy as the model including PP (0.96 for both). The selected RF model correctly predicted 98% (585/599) of the non-foraging habitat and 91% (269/294) of the foraging habitat, as defined in this study. Predictions were qualitatively consistent with known leatherback turtle foraging habitat (Fig. S1, Benson *et al.*, 2011).

*DGN fishing locations (Maxent)*

Based on a comparison of the three statistics used to evaluate the Maxent predictions (AUC, gain, and sensitivity) and response curves, we selected a model with hinge and quadratic features (HQ), using all variables, and a regularization parameter value of 0.1 as the best

**Table 5.** Estimated coefficients and approximate 95%PI for the best logistic regression model (Model 3) for the analysis of predicting the departure of leatherback turtles from the PLCA.

	Median	2.5%	97.5%
Intercept	1.37	-5.37	8.13
PDO	-7.86	-11.04	-5.15
UW48mean_60d	15.54	11.89	19.89
s	9.12	5.22	8.13

UW48mean\_60d = mean upwelling at 48°N over 60 days, s = standard deviation of the individual random effects.

performing model. This model had an AUC value of the test data of 0.84 (the probability that a randomly selected presence point was ranked higher than a randomly selected background point),  $\exp(\text{gain})$  without the random number variable of 2.35 (how much greater the average likelihood was at the presence point compared with a random background point), and sensitivity of 0.63 (the probability of correctly predicting presence of DGN fishing in the test data).

For both variable selection statistics (contribution and importance), SST lagged by 30 days (SST30) and latitude were the two most important variables. Among the six most useful variables (i.e., SST30, SST14, SST0, Depth, Longitude, and Latitude), SST14 appeared to have the most useful information by itself (the highest training gain) whereas latitude appeared to have the most information that is absent in the other variables (decreased the gain the most when it was omitted). The response curve for SST30 indicated that a likelihood of a DGN set increased with 30-days lagged SST, especially above 16°C. The predicted DGN fishery for 2001–2010 indicated a relatively high likelihood of fishing nearshore, perhaps moving southward in the summer and fall months (Fig. S2).

#### *Co-occurrence of leatherback turtle foraging habitat and DGN fishing*

The maximum likelihood of co-occurrence of leatherback turtle foraging habitat and DGN fishing gear within the study area was highest during September/October and lowest during November (Fig. 5). The variability among years was greatest during the first half of September. The variability decreased during October and November. The mean co-occurrence likelihood for the 2001–2010 period indicated that a high likelihood of co-occurrence was found in nearshore areas of central California during September and October (Fig. 6). In contrast, offshore areas exhibited

a low co-occurrence likelihood mostly because of the low likelihood of turtle foraging habitat.

## DISCUSSION

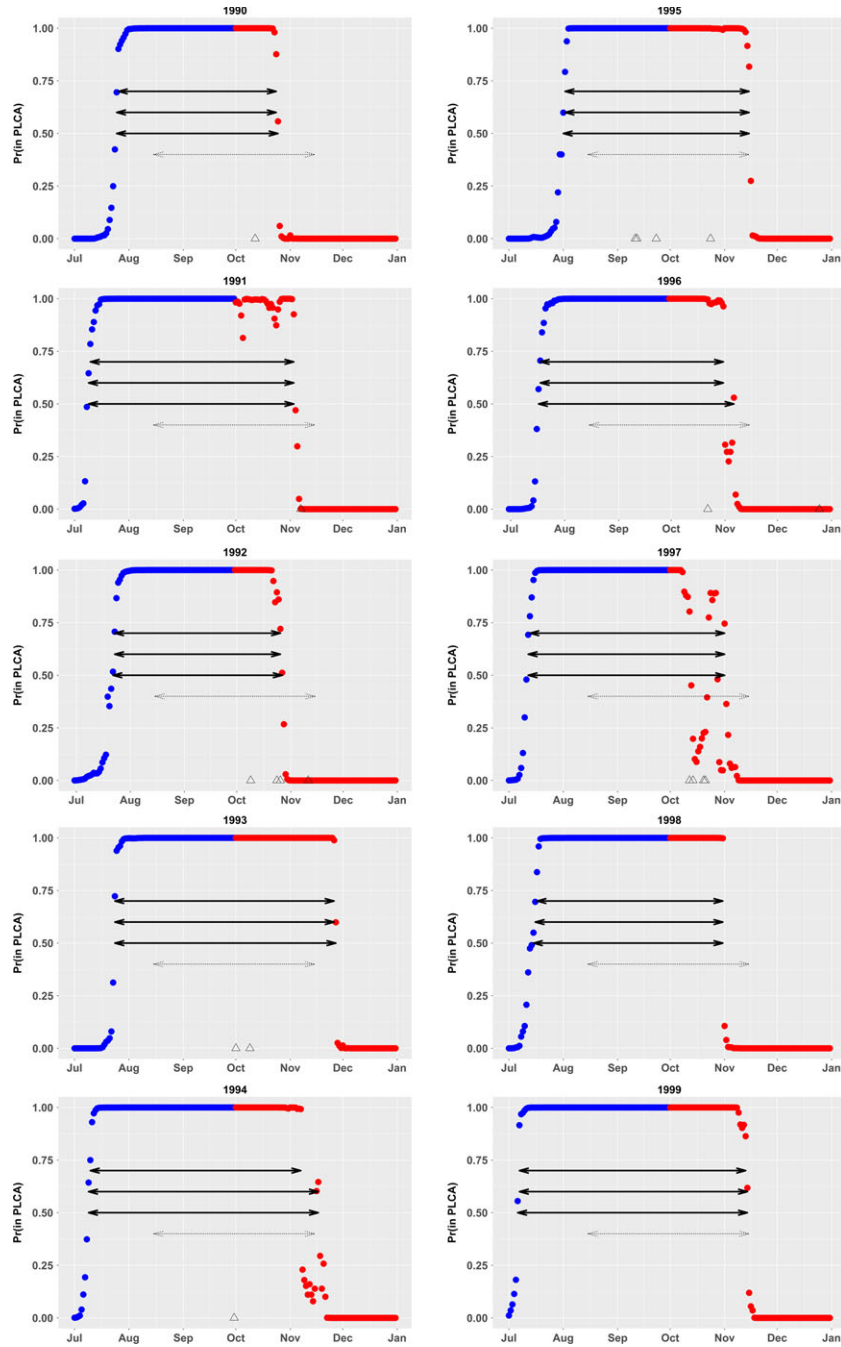
### *Presence of leatherback turtles in the PLCA*

Different sets of environmental variables affected entry to and departure from the PLCA by leatherback turtles. Likelihood of entry to PLCA by leatherback turtles increased as the season progressed in early summer and with an increasing cumulative UW index at 39N. The likelihood of entry, however, decreased with increasing variability of the UW index at 36N over 60 days. This is consistent with our understanding of leatherback turtle behavior, where strong and consistent upwelling in the spring followed by relaxation of upwelling is necessary to create favorable conditions for the turtles (Benson *et al.*, 2007, 2011).

In contrast, departure from the PLCA was linked to various statistics of the upwelling index at a higher latitude (48N) than for entry (36N and 39N). As the upwelling index at 48N decreased, the probability of departure increased (or probability of presence decreased). This result might be caused by the three tracks in the northern part of the study area. The RF analysis without these tracks resulted in the upwelling index at 39N to be important (results not shown). A larger sample size will be necessary to tease out the effects of spatial variability of tracks within the study area. Overall, the model predictions fit well with our understanding of the timing of leatherback turtle occurrence in the PLCA. The probability of leatherback turtle occurrence increased in mid-July, before the current mid-August PLCA closure period (Fig. 5). The probability decreased in mid-November broadly coinciding with the current closure (Fig. 4).

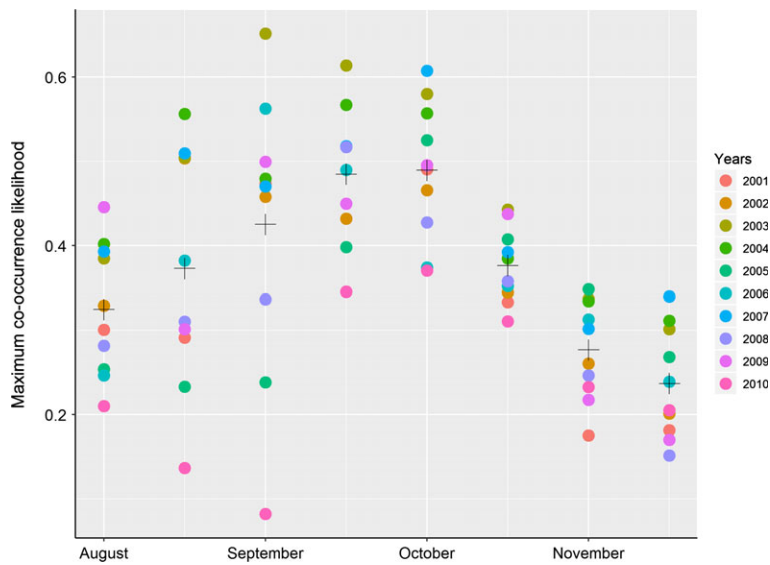
The current time-area closure for the DGN fishery along the west coast of the US seems to be effective. Had the fixed time-area closure regulation existed in the 1990s, 18 of 19 observed bycatch events between August 15 and November 15 could have been avoided. In this study, we developed a statistical approach to model the presence of leatherback turtles in the PLCA. For example, the DGN fishery might be restricted in the PLCA when the probability of leatherback turtle occurrence is greater than some threshold value. This could result in an annual fishery closure period that is longer or shorter than the current fixed closure design. Using probability thresholds of 0.5, 0.6, or 0.7 to dynamically close the fishery would have avoided 18 of the observed bycatch events (the same as the existing closure), although specifics differed for 2 of the years observed during

**Figure 4.** Predicted median probabilities of presence of leatherback turtles in the PLCA from 1990 to 1999. Blue and red points indicate whether entry or departure models, respectively, were used. Horizontal dashed arrows at  $P = 0.4$  indicate the current fishery closure period, whereas possible closures based on the predicted probabilities of turtle presence are shown at respective probabilities (0.5, 0.6 and 0.7). Triangle indicates the date of observed bycatch within the PLCA.



that time period. Specifically, four additional bycatch events would have occurred (1 in 1991 and 3 in 1992) if the above probability approach had been used instead of the existing PLCA closure (Fig. 4).

The probabilistic approach would not, however, have shortened the closure duration. Further, there is inherent uncertainty in probabilistic predictions for any given year, although the posterior distributions of



**Figure 5.** Temporal patterns of maximum co-occurrence likelihood between DGN fishing effort and leatherback turtle foraging habitat for 2-week periods between August and November from 2001 to 2010. Plus signs indicate the mean for each time period.

the coefficients could be used to assess uncertainty explicitly. Overall, the results of our model of leatherback presence in the PLCA suggest that the current August 15 to November 15 closure is the shortest and most effective for protecting leatherback turtles in the PLCA while allowing fishing during low-risk bycatch periods.

#### *Co-occurrence of leatherback turtles and DGN fishing*

We found that telemetry data and the RF approach could be used to predict foraging habitat of leatherback turtles throughout the entire PLCA when some foraging areas in this region are known *a priori*. Known foraging habitats along the coast were predicted to be good foraging habitat even though spatial reference variables (latitude and longitude) were not included in the predictive model (Fig. 6). Areas identified as a foraging habitat in this study corresponded well to areas where foraging was inferred from telemetry studies, in which a different approach was used (Benson *et al.*, 2011). DGN fishing effort predictions using Maxent appeared less precise, possibly because only one dynamic variable, SST, was available. The response curve for SST30 indicated that fishing occurred in a narrow SST band, especially lagged by 30 days. Fishers might be cueing in on certain SST values based on their experience with their target catch (swordfish and thresher sharks). Additional environmental variables might increase the precision of these models, and recent advances in data-assimilative ocean circulation models (e.g., Moore *et al.*, 2011) may allow the use of model-based habitat predictors, which have shown promise for predicting cetacean distributions in the California Current

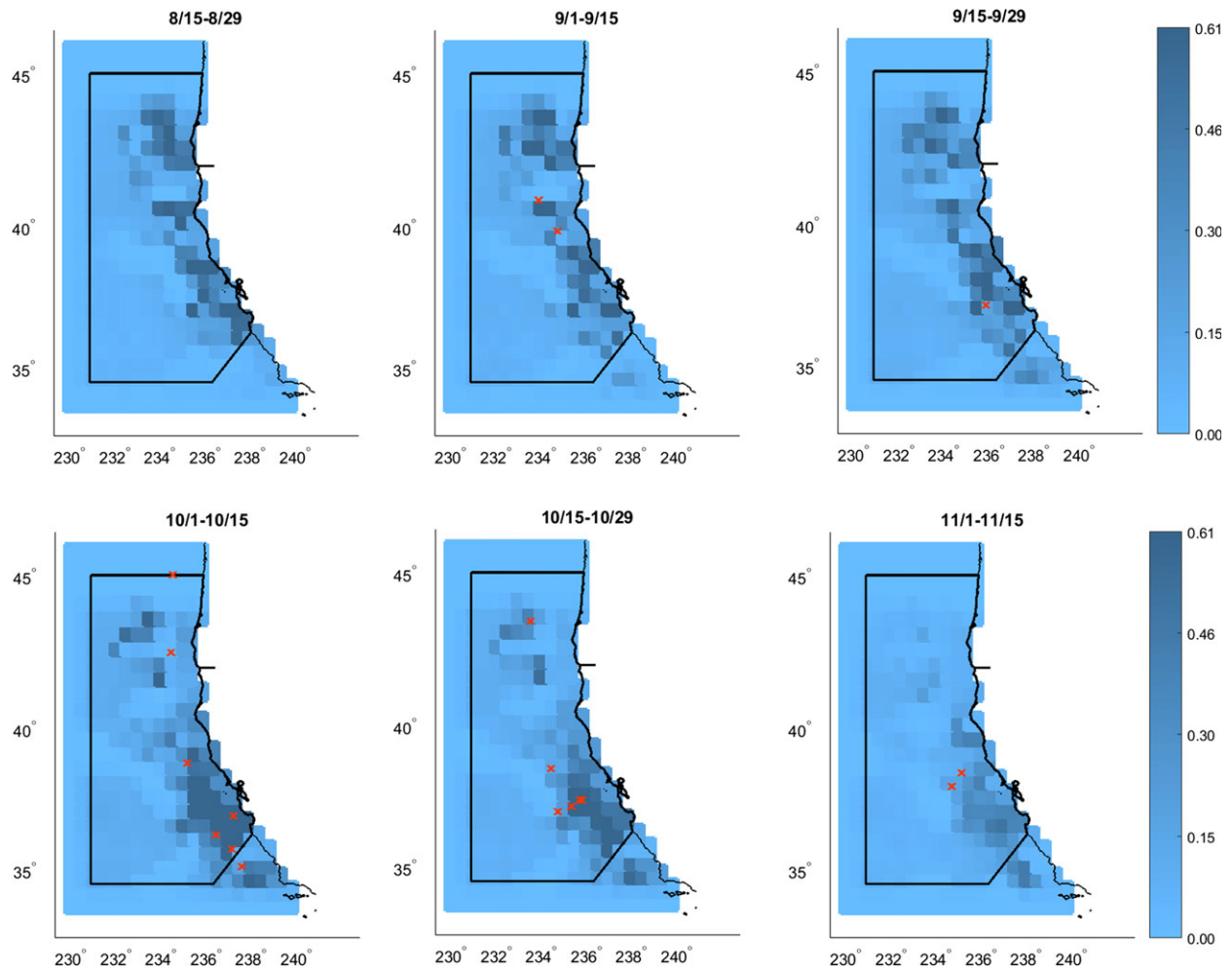
Ecosystem (Becker *et al.*, 2016). Economic and logistic factors are also likely to play a role in the distribution of fishing effort, potentially masking environmental patterns (Soykan *et al.*, 2014).

Although there is uncertainty in both of the above models and they were developed from data sets spanning different time periods, the combined model of potential overlap between leatherback foraging habitat and fishing effort provides a starting point for evaluating finer-scale spatiotemporal patterns of potential bycatch risk to leatherback turtles within our study area. Months with lower documented bycatch rates (August and November) were also predicted to have low overlap in our combined model. Further, most of the actual bycatch events observed during 1990–2000 were located in areas of greater predicted overlap (Fig. 6). In particular, overlap was predicted to be high during late September and October off central California, where and when the majority of observed leatherback bycatch events took place. However, we emphasize that this analysis only considers overlap between foraging habitat of leatherback turtles and the DGN fishery. The late October and November bycatch events that are in areas of low predicted overlap suggest that bycatch also occurs when turtles left nearshore foraging areas and were transiting through DGN fishing areas.

The ability of our models to capture at least some of the documented bycatch patterns suggests that there may be options for dynamic management of the DGN fishery in the future. However, more comprehensive models that include both foraging and transiting behavior of leatherback turtles, coupled with



**Figure 6.** Predicted mean overlap likelihood for six 2-week spans for 1990–2000 during the current DGN closure period. The darker color indicates a higher likelihood and vice versa. Red x's indicate locations of observed bycatch events and 230° longitude corresponds to 130°W.



simulation analyses to address model uncertainties, will be required to allow the evaluation of potential dynamic management strategies. Model-based predictions should also be validated with independent data sets, such as surveys of fishing gear locations (or through vessel monitoring system) and leatherback turtles. These additional analyses may require new data sets that include systematic information on both presence and absence of turtles and fishing effort.

Fishery independent survey data on the distribution of by-caught species, such as sea turtles, have been shown to be useful in understanding fishery bycatch, especially when combined with fishery dependent data (Murray and Orphanides, 2013). Design-based studies, e.g., aerial line-transect surveys conducted over large areas and sufficiently long time

periods, are essential to capture interannual and seasonal variability in leatherback turtle distributions. Telemetry data can also provide information on leatherback turtle movements and inferred behavior (e.g., Benson *et al.*, 2011; Shillinger *et al.*, 2011). Additional other presence/absence data can provide more precise predictions of species distribution based on environment and allow estimation of densities (Aarts *et al.*, 2008).

Similarly, fishery logbooks only provide presence data, because there is no record of areas that the vessel passed through without making a set. True absence data should be collected whenever possible (Phillips *et al.*, 2009; Wisz and Guisan, 2009; Aarts *et al.*, 2012), for example, by obtaining tracks of fishing vessels to provide information on locations where fishers

could have set their gear but did not. If this is not possible, an alternate approach is the creation of pseudo-absence points (e.g., Guisan *et al.*, 2002; Stokland *et al.*, 2011; Zydalis *et al.*, 2011; Barbet-Massin *et al.*, 2012), but care must be taken when generating pseudo-absences, as this can affect the accuracy of Maxent predictions (Phillips *et al.*, 2009; VanDerWal *et al.*, 2009).

The results of our study provide a foundation for future explorations of dynamic ocean management scenarios for the DGN fishery that would protect leatherback turtles and other species. However, our results suggest that such a dynamic management framework will need to be dynamic in both space and time, which requires more precise and comprehensive models of leatherback turtle behavior and fishing effort distributions than possible with the currently available data. This is likely caused, in part, by the highly variable nature of the California Current Ecosystem, compared to, for example, the central North Pacific, where simple models of sea turtle and fishery overlap were developed to estimate near-real time bycatch risk within the fishing area (Howell *et al.*, 2008, 2015).

The collection of adequate new data to improve predictive models of leatherback turtles and the DGN fishery will probably require multiple years of dedicated research. Therefore, alternative tools for allowing swordfish fishing within the California Current Ecosystem while minimizing bycatch risk should continue to be explored. Changes in hook and bait types have reduced loggerhead and leatherback turtle bycatch in Hawaii-based longline fisheries while retaining or increasing the target species catch rate (Gilman *et al.*, 2007). Studies of the vertical and horizontal distributions of target species (e.g., Abecassis *et al.*, 2012; Sepulveda *et al.*, 2014) and protected species may allow the development of alternative gear types to maximize exposure to target species and minimize risk to protected species. For example, the bycatch of air-breathing species such as sea turtles and marine mammals potentially can be reduced if the fishing gear is deployed deeper within the water column. Recent studies on deep-set buoy gear targeting swordfish show promise if catch rates can become economically viable (Sepulveda *et al.*, 2014).

In conclusion, the results of our study indicate that the current PLCA closure period is effective for reducing leatherback turtle bycatch in the DGN fishery. Model predictions confirmed that the current PLCA eliminates most of the spatial and temporal bycatch risk to leatherback turtles. With additional data, finer-

scale dynamic refinements to this closure are possible, but the challenges of implementing and enforcing such dynamic management are complex, given the temporal and spatial scales that vessel captains base their fishing decisions upon. Additional data and expanded modeling studies will be required to develop and test potential dynamic management scenarios.

## ACKNOWLEDGEMENTS

Satellite telemetry transmitters were deployed on leatherback turtles under Endangered Species Act permit numbers 1159, 1227, and 1596 using approved animal handling protocols and in conformance with all applicable laws. We thank the data managers at Fisheries Resources Division of the Southwest Fisheries Science Center for converting DGN fishery logbook data into an electronic format and making them available. We appreciate Jeffrey Seminoff, Jim Carretta, and anonymous reviewers for providing constructive comments, which improved the manuscript. The authors acknowledge that there is no conflict of interest to declare.

## REFERENCES

- Aarts, G., MacKenzie, M., McConnell, B., Fedak, M. and Matthiopoulos, J. (2008) Estimating space-use and habitat preference from wildlife telemetry data. *Ecography* **31**:140–160.
- Aarts, G., Fieberg, J. and Matthiopoulos, J. (2012) Comparative interpretation of count, presence-absence and point methods for species distribution models. *Methods Ecol. Evol.* **3**:177–187.
- Abecassis, M., Dewar, H., Hawn, D. and Polovina, J. (2012) Modeling swordfish daytime vertical habitat in the North Pacific Ocean from pop-up archival tags. *Mar. Ecol. Prog. Ser.* **452**:219–236.
- Alverson, D.L., Freeberg, M.H., Pope, J.G. and Murawski, S.A. (1994). A global assessment of fisheries bycatch and discards. FAO Fisheries Technical Paper 339: 233 pp. URL <http://www.fao.org/DOCREP/003/T4890E/T4890E00.HTM#TOC> [accessed 29 August 2016].
- Baker, C.S., Lukoschek, V., Lavery, S. *et al.* (2006) Incomplete reporting of whale, dolphin and porpoise “bycatch” revealed by molecular monitoring of Korean markets. *Anim. Conserv.* **9**:474–482.
- Bakun, A. (1973) Coastal upwelling indices, West coast of North America 1946–1971. *NOAA Tech. Rep. NMFS* **671**: 103 pp.
- Bakun, A., McLain, D.R. and Mayo, F. (1974) Mean annual cycle of coastal upwelling off western North America as observed from surface measurements. *Fish. Bull.* **72**:843–844.
- Barbet-Massin, M., Jiguet, F., Albert, C.H. and Thuiller, W. (2012) Selecting pseudo-absences for species distribution models: how, where and how many?. *Methods Ecol. Evol.* **3**:327–338.
- Becker, E., Forney, K., Fiedler, P. *et al.* (2016) Moving towards dynamic ocean management: how well do

- modeled ocean products predict species distributions? *Remote Sens.* **8**:149.
- Benson, S.R., Forney, K.A., Harvey, J.T., Carretta, J.V. and Dutton, P.H. (2007) Abundance, distribution, and habitat of leatherback turtles (*Dermochelys coriacea*) off California, 1990–2003. *Fish. Bull.* **105**:337–347.
- Benson, S.R., Eguchi, T., Foley, D.G. *et al.* (2011) Large-scale movements and high-use areas of western Pacific leatherback turtles, *Dermochelys coriacea*. *Ecosphere* **2** Article 84.
- Block, B.A., Jonsen, I.D., Jorgensen, S.J. *et al.* (2011) Tracking apex marine predator movements in a dynamic ocean. *Nature* **475**:86–90.
- Bograd, S.J., Schroeder, I., Sarkar, N., Qiu, X., Sydeman, W.J. and Schwing, F.B. (2009) Phenology of coastal upwelling in the California Current. *Geophys. Res. Lett.* **36**:1–5.
- Breiman, L. (2001) Random forests. *Mach. Learn* **45**:5–32.
- Carretta, J.V. and Barlow, J. (2011) Long-term effectiveness, failure rates, and “dinner bell” properties of acoustic pingers in a gillnet fishery. *Mar. Technol. Soc. J.* **45**:7–19.
- Carretta, J.V. and Moore, J.E. (2014) Recommendations for pooling annual bycatch estimates when events are rare. *NOAA Tech. Memo. SWFSC* **528**: 11 pp.
- Carretta, J.V., Price, T., Petersen, D. and Read, R. (2004) Estimates of marine mammal, sea turtle, and seabird mortality in the California drift gillnet fishery for swordfish and thresher shark, 1996–2002. *Mar. Fish. Rev.* **66**:21–30.
- Carretta, J.V., Barlow, J. and Enriquez, L. (2008) Acoustic pingers eliminate beaked whale bycatch in a gill net fishery. *Mar. Mamm. Sci.* **24**:956–961.
- Carretta, J.V., Enriquez, L. and Villafna, C. (2014) Marine mammal, sea turtle, and seabird bycatch in California gillnet fisheries in 2012. *NOAA Tech. Memo. SWFSC* **526**: 16 pp.
- Chelton, D., Bernal, P. and McGowan, J. (1982) Large-scale interannual physical and biological interaction in the California current. *J. Mar. Res.* **40**:1095–1125.
- Cohen, J. (1960) A coefficient of agreement of nominal scales. *Educ. Psychol. Meas.* **20**:37–46.
- Cox, T.M., Lewison, R.L., Zydelski, R., Crowder, L.B., Safina, C. and Read, A.J. (2007) Comparing effectiveness of experimental and implemented bycatch reduction measures: the ideal and the real. *Conserv. Biol.* **21**:1155–1164.
- Curtis, K.A., Moore, J.E. and Benson, S.R. (2015) Estimating limit reference points for western Pacific leatherback turtles (*Dermochelys coriacea*) in the U.S. west coast EEZ. *PLoS One* **10**:e0136452.
- Dewar, H., Prince, E.D., Musyl, M.K. *et al.* (2011) Movements and behaviors of swordfish in the Atlantic and Pacific Oceans examined using pop-up satellite archival tags. *Fish Oceanogr.* **20**:219–241.
- Ducet, N., Le Traon, P.Y. and Reverdin, G. (2000) Global high-resolution mapping of ocean circulation from TOPEX/Poseidon and ERS-1 and -2. *J. Geophys. Res.* **105**:19477–19498.
- Dutton, P.H. and Squires, D. (2011) A holistic strategy for Pacific sea turtle conservation. In: Conservation and Sustainable Management of Sea Turtles in the Pacific Ocean. P.H. Dutton, D. Squires & A. Mahfuzuddin (eds) Honolulu: University of Hawaii Press, pp. 37–59.
- Eayrs, S. (2007) A Guide to Bycatch Reduction in Tropical Shrimp-Trawl Fisheries. Revised Edition. Rome: FAO. 108 pp. URL <http://www.fao.org/docrep/015/a1008e/a1008e.pdf> [accessed 29 August 2016].
- Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E. and Yates, C.J. (2011) A statistical explanation of MaxEnt for ecologists. *Divers. Distrib.* **17**:43–57.
- Ferguson, M.C., Barlow, J., Reilly, S.B. and Gerrodette, T. (2005) Predicting Cuvier’s (*Ziphius cavirostris*) and *Mesoplodon* beaked whale population density from habitat characteristics in the eastern tropical Pacific Ocean. *J. Cetacean Res. Manag.* **7**:287–299.
- Forney, K.A. (2000) Environmental models of cetaceans abundance: reducing uncertainty in population trends. *Conserv. Biol.* **14**:1271–1286.
- Forney, K.A., Kobayashi, D.R., Johnston, D.W., Marchetti, J.A. and Marsik, M.G. (2011) What’s the catch? Patterns of cetacean bycatch and depredation in the Hawaii-based pelagic longline fisheries. *Mar. Ecol.* **32**:380–391.
- Gardner, B., Sullivan, P., Epperly, S. and Morreale, S. (2008) Hierarchical modeling of bycatch rates of sea turtles in the western North Atlantic. *Endanger. Species Res.* **5**:279–289.
- Gelman, A., Carlin, J.B., Stern, H.S., Dunson, D.B., Vehtari, A. and Rubin, D.B. (2014) Bayesian data analysis, 3rd edn. Boca Raton, FL: CRC Press.
- Gilman, E., Brothers, N. and Kobayashi, D.R. (2005) Principles and approaches to abate seabird by-catch in longline fisheries. *Fish Fish.* **6**:35–49.
- Gilman, E., Zollett, E., Beverly, S. *et al.* (2006) Reducing sea turtle by-catch in pelagic longline fisheries. *Fish and Fisheries* **7**:2–23.
- Gilman, E., Kobayashi, D., Swenarton, T., Brothers, N., Dalzell, P. and Kinankelly, I. (2007) Reducing sea turtle interactions in the Hawaii-based longline swordfish fishery. *Biol. Conserv.* **139**:19–28.
- Gilman, E., Kobayashi, D. and Chaloupka, M. (2008) Reducing seabird bycatch in the Hawaii longline tuna fishery. *Endanger. Species Res.* **5**:309–323.
- Graham, W.M., Pagès, F. and Hamner, W.M. (2001) A physical context for gelatinous zooplankton aggregations: a review. *Hydrobiologia* **451**:199–212.
- Graham, T.R., Harvey, J.T., Benson, S.R., Renfree, J.S. and Demer, D.A. (2010) The acoustic identification and enumeration of scyphozoan jellyfish, prey for leatherback sea turtles (*Dermochelys coriacea*), off central California. *ICES J. Mar. Sci.* **67**:1739–1748.
- Guisan, A., Edwards, T.C. and Hastie, T. (2002) Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecol. Modell.* **157**:89–100.
- Hijmans, R.J., Phillips, S., Leathwick, J., Elith, J. (2014) Species distribution modeling. <https://cran.r-project.org/> [accessed 29 August 2016].
- Hobday, A.J. and Hartmann, K. (2006) Near real-time spatial management based on habitat predictions for a longline bycatch species. *Fish. Manag. Ecol.* **13**:365–380.
- Hothorn, T., Hornik, K. and Zeileis, A. (2006) Unbiased recursive partitioning: a conditional inference framework. *J. Comput. Graph. Stat.* **15**:651–674.
- Howell, E.A., Kobayashi, D.R., Parker, D.M., Balaz, G.H. and Polovina, J.J. (2008) TurtleWatch: a tool to aid in the bycatch reduction of loggerhead turtles *Caretta caretta* in the Hawaii-based pelagic longline fishery. *Endanger. Species Res.* **5**:267–278.

- Howell, E.A., Hoover, A., Benson, S.R. *et al.* (2015) Enhancing the TurtleWatch product for leatherback sea turtles, a dynamic habitat model for ecosystem-based management. *Fish Oceanogr.* **24**:57–68.
- Janitzka, S., Strobl, C. and Boulesteix, A.-L. (2013) An AUC-based permutation variable importance measure for random forests. *BMC Bioinformatics* **14**:119.
- Johnson, D.S., London, J.M., Lea, M.-A. and Durban, J.W. (2008) Continuous-time correlated random walk model for animal telemetry data. *Ecology* **89**:1208–1215.
- Jonsen, I.D., Myers, R.A. and Flemming, J.M. (2003) Meta-analysis of animal movement using state-space models. *Ecology* **84**:3055–3063.
- Jonsen, I.D., Flemming, J.M. and Myers, R.A. (2005) Robust state–space modeling of animal movement data. *Ecology* **86**:2874–2880.
- Julian, F. and Beeson, M. (1998) Estimates of marine mammal, turtle, and seabird mortality for two California gillnet fisheries: 1990–1995. *Fish. Bull.* **96**:271–284.
- Komoroske, L.M. and Lewison, R.L. (2015) Addressing fisheries bycatch in a changing world. *Front. Mar. Sci.* **2**:1–11.
- Kuhn, M. (2013) Package “caret”: Classification and Regression Training. R package version 6.0-64. <http://caret.r-forge.r-project.org/> [accessed 29 August 2016].
- Larsen, F., Eigaard, O.R. and Tougaard, J. (2007) Reduction of harbour porpoise (*Phocoena phocoena*) bycatch by iron-oxide gillnets. *Fish. Res.* **85**:270–278.
- Lewison, R., Hobday, A.J., Maxwell, S. *et al.* (2015) Dynamic ocean management: identifying the critical ingredients of dynamic approaches to ocean resource management. *Bioscience* **65**:486–498.
- Lynn, R.J. and Simpson, J.J. (1987) The California current system: the seasonal variability of its physical characteristics. *J. Geophys. Res.* **92**:12,947–12,966.
- Mann, K.H. and Lazier, J.R.N. (2006) Dynamics of Marine Ecosystems: Biological-Physical Interactions in the Oceans 3rd edn. Cambridge, MA: Blackwell Publishing.
- Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M. and Francis, R.C. (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull. Am. Meteorol. Soc.* **78**:1069–1079.
- Martin, S.L., Stohs, S.M. and Moore, J.E. (2015) Bayesian inference and assessment for rare-event bycatch in marine fisheries : a drift gillnet fishery case study. *Ecol. Appl.* **25**:416–429.
- Maxwell, S.M., Hazen, E.L., Lewison, R.L. *et al.* (2015) Dynamic ocean management: defining and conceptualizing real-time management of the ocean. *Mar. Policy* **58**:42–50.
- Moore, A.M., Arango, H.G., Broquet, G., Powell, B.S., Weaver, A.T. and Zavala-Garay, J. (2011) The Regional Ocean Modeling System (ROMS) 4-dimensional variational data assimilation systems. Part I – System overview and formulation. *Prog. Oceanogr.* **91**:34–49.
- Morales, J.M., Haydon, D.T., Frair, J., Holsinger, K.E. and Fryxell, J.M. (2004) Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology* **85**:2436–2445.
- Murray, K.T. (2009) Characteristics and magnitude of sea turtle bycatch in US mid-Atlantic gillnet gear. *Endanger. Species Res.* **8**:211–224.
- Murray, K. and Orphanides, C. (2013) Estimating the risk of loggerhead turtle *Caretta caretta* bycatch in the US mid-Atlantic using fishery-independent and -dependent data. *Mar. Ecol. Prog. Ser.* **477**:259–270.
- National Marine Fisheries Service (2013) Biological Opinion on the continued management of the drift gillnet fishery under the Fishery Management Plan for U.S. west coast fisheries for highly migratory species. URL [http://www.west-coast.fisheries.noaa.gov/publications/protected\\_species/marine\\_mammals/memo\\_signed\\_dgn\\_biop\\_050213.pdf](http://www.west-coast.fisheries.noaa.gov/publications/protected_species/marine_mammals/memo_signed_dgn_biop_050213.pdf) [accessed 30 August 2016].
- Phillips, S.J. and Dudík, M. (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography (Cop.)* **31**:161–175.
- Phillips, S.J., Anderson, R.P. and Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecol. Modell.* **190**:231–259.
- Phillips, S.J., Dudík, M., Elith, J. *et al.* (2009) Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecol. Appl.* **19**:181–197.
- Plummer, M. (2015) Bayesian graphical models using MCMC. <http://mcmc-jags.sourceforge.net> [accessed 29 August 2016].
- R Core Team (2014) R: A Language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing. <http://www.R-project.org> [accessed 29 August 2016].
- Read, A.J. (2008) The looming crisis: interactions between marine mammals and fisheries. *J. Mammal.* **89**:541–548.
- Read, A.J., Drinker, P. and Northridge, S. (2006) Bycatch of marine mammals in U.S. and global fisheries. *Conserv. Biol.* **20**:163–169.
- Rivera, K. and Wohl, K.D. (1999) The FAO seabird initiative – international efforts to reduce seabird bycatch in the longline fisheries: what does that mean at home? An Alaskan perspective. *Mar. Technol. Soc. J.* **33**:85–87.
- Roe, J.H., Morreale, S.J., Paladino, F.V. *et al.* (2014) Predicting bycatch hotspots for endangered leatherback turtles on longlines in the Pacific Ocean. *Proc. R. Soc. B* **281**:20132559.
- Sampson, D.B. (2011) The accuracy of self-reported fisheries data: Oregon trawl logbook fishing locations and retained catches. *Fish. Res.* **112**:59–76.
- Schwing, F.B. and Mendelssohn, R. (1997) Increased coastal upwelling in the California Current System. *J. Geophys. Res.* **102**:3421–3438.
- Schwing, F., Murphree, T. and Green, P. (2002) The Northern Oscillation Index (NOI): a new climate index for the northeast Pacific. *Prog. Oceanogr.* **53**:115–139.
- Seminoff, J.A., Zárata, P., Coyne, M.S. *et al.* (2008) Post-nesting migrations of Galápagos green turtles *Chelonia mydas* in relation to oceanographic conditions: integrating satellite telemetry with remotely sensed ocean data. *Endanger. Species Res.* **4**:57–72.
- Sepulveda, C.A., Heberer, C. and Aalbers, S.A. (2014) Development and trial of deep-set buoy gear for sword fish, *Xiphias gladius*, in the Southern California Bight. *Mar. Fish. Rev.* **76**:28–36.
- Shillinger, G.L., Swithenbank, A.M., Bailey, H. *et al.* (2011) Vertical and horizontal habitat preferences of post-nesting leatherback turtles in the South Pacific Ocean. *Mar. Ecol. Prog. Ser.* **422**:275–289.
- Sims, M., Cox, T. and Lewison, R. (2008) Modeling spatial patterns in fisheries bycatch: improving bycatch maps to aid fisheries management. *Ecol. Appl.* **18**:649–661.

- Soykan, C.U., Eguchi, T., Kohin, S. and Dewar, H. (2014) Prediction of fishing effort distributions using boosted regression trees. *Ecol. Appl.* **24**:71–83.
- Starbird, C.H., Baldrige, A. and Harvey, J.T. (1993) Seasonal occurrence of leatherback sea turtles (*Dermochelys coriacea*) in the Monterey Bay region, with notes on other sea turtles, 1986-1991. *Calif. Fish Game* **79**:54–62.
- Stokland, J.N., Halvorsen, R. and Støa, B. (2011) Species distribution modelling—Effect of design and sample size of pseudo-absence observations. *Ecol. Modell.* **222**:1800–1809.
- Strobl, C., Boulesteix, A.-L., Zeileis, A. and Hothorn, T. (2007) Bias in random forest variable importance measures: illustrations, sources and a solution. *BMC Bioinformatics* **8**:25.
- Strobl, C., Boulesteix, A.-L., Kneib, T., Augustin, T. and Zeileis, A. (2008) Conditional variable importance for random forests. *BMC Bioinformatics* **9**:307.
- Tapilatu, R.F., Dutton, P.H., Tiwari, M. *et al.* (2013) Long-term decline of the western Pacific leatherback, *Dermochelys coriacea*: a globally important sea turtle population. *Ecosphere* **4**, Article 25.
- VanDerWal, J., Shoo, L.P., Graham, C. and Williams, S.E. (2009) Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? *Ecol. Modell.* **220**:589–594.
- Wallace, B.P., Lewison, R.L., McDonald, S.L. *et al.* (2010) Global patterns of marine turtle bycatch. *Conserv. Lett.* **3**:131–142.
- Wisz, M.S. and Guisan, A. (2009) Do pseudo-absence selection strategies influence species distribution models and their predictions? An information-theoretic approach based on simulated data. *BMC Ecol.* **9**:8.
- Xie, L. and Hsieh, W.W. (1995) The global distribution of wind-induced upwelling. *Fish Oceanogr.* **4**:52–67.
- Zydelis, R., Lewison, R.L., Shaffer, S.A. *et al.* (2011) Dynamic habitat models: using telemetry data to project fisheries bycatch. *Proc. R. Soc. B Biol. Sci.* **278**:3191–3200.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Predicted leatherback turtle foraging habitat likelihood during summer/autumn 2007.

**Figure S2.** Predicted DGN habitat likelihood during summer/autumn 2007. The dark colors indicate higher likelihoods and vice versa.